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Abstract

Most hypotheses related to the evolution of female-biased extreme sexual size dimorphism (SSD) attribute the differences in the size of each sex to selection for reproduction, either through selection for increased female fecundity or selection for male increased mobility and faster development. Very few studies, however, have tested for direct fitness benefits associated with the latter – small male size. *Mecaphesa celer* is a crab spider with extreme SSD, whose males are less than half the size of females and often weigh 10 times less. Here, we test the hypotheses that larger size in females and smaller size in males are sexually selected through differential pre- and postcopulatory reproductive benefits. To do so, we tested the following predictions: matings between small males and large females are more likely to occur due to mate choice; females mated to small males are less likely to accept second copulation attempts; and matings between small males and large females will result in larger clutches of longer-lived offspring. Following staged mating trials in the laboratory, we found no support for any of our predictions, suggesting that SSD in *M. celer* may not be driven by pre- or post-reproductive fitness benefits to small males.

Keywords: clutch success, fitness benefits, offspring survival, Mecaphesa celer, size, Thomisidae

Introduction

The average body size of most animals at sexual maturation results from the delicate balance between selection for survival and selection for reproduction (Stillwell et al. 2010). In species with sexual size dimorphism (SSD), the size difference between the sexes can be attributed to these two sources of selection acting differently upon each sex, and reaching equilibrium at different points (SSD equilibrium model: Blanckenhorn 2005). While sexually dimorphic traits, such as male ornaments and weapons, are a classic example of strong selection for reproduction acting upon males only (Andersson & Simmons 2006), physiological constraints and genetic correlations are expected to maintain the size of both sexes within similar ranges (the null hypothesis of size equality – Hedrick & Temeles 1989; Andersson 1996). Differences in female and male sizes are, however, not only very common, but sometimes quite extreme, such as in many examples of female-biased SSD (Stillwell et al. 2010). The evolution of such female-biased SSD must reflect selection acting in opposing directions, or at least with different intensities, in males and females (Blanckenhorn 2000; Blanckenhorn 2005; Kuntner & Elgar 2014).

Selection for reproduction in females is often associated to increased egg production (Clutton-Brock 1991; Stillwell et al. 2010). Fecundity benefits related to a larger female body size are well documented across various animal groups (e.g., mammal: Fokidis et al. 2007; birds: Sedinger et al. 1995; reptiles: Hendry et al. 2014; insects: Honěk, 1993 and spiders: Beck & Connor 1992; Prenter et al. 1999). As such, selection for increased fecundity is often assumed to be the main mechanism leading to maintenance and/or exaggeration of female size in species with female-biased SSD (see Blanckenhorn 2005 and references therein, Stillwell et al. 2010).

In contrast to our understanding of selection for increased female size, in most taxa little is understood about how selection might act to reduce or maintain small male size (Blanckenhorn 2005). The role of selection in the reduction or maintenance of small male size

is typically attributed to an increase in the chances of a male's encounter with suitable females, or a reduction in the risks associated with such encounters (Ghiselin 1974; Vollrath 1998). It is hypothesized that small males may benefit by being more agile (e.g., midges – Crompton et al. 2003), or by reaching sexual maturation faster than females (e.g., paedomorphic boneworms – Rouse et al. 2004), or faster than larger male competitors (Kasumovic & Andrade 2009). Once a suitable female is encountered, small males may also benefit through opportunistic cohabitation and kleptoparasitism (e.g., golden orb-web spiders – Kasumovic et al. 2006).

Spiders are the only taxon where males are often less than half the size of females, with such extreme SSD having evolved independently in at least seven families (Scharff & Coddington 1997; Hormiga et al. 2000). Three not mutually exclusive hypotheses are commonly associated to the evolution of small male size in spiders. The first is adaptive protandry, where males mature earlier than females and benefit from minimum competition for access to sexually receptive females, being particularly adaptive in species where females mate only once and/or where there is first male sperm priority (Maklakov et al. 2004; Kasumovic & Andrade 2009). The second is the differential male mortality hypothesis, which predicts that in species whose adults have distinct lifestyles (such as sedentary orb-weaving females and wandering males), small size would allow males to suffer smaller mortality risks (Vollrath & Parker 1992; De Mas et al. 2009). Finally, the adaptive sexual cannibalism hypothesis predicts that small male size increases the probability of a male being eaten by a female postcopulation, which is adaptive in species where the consumption of the male by a female immediately after copulation can increase the reproductive success of both sexes (Andrade 1996; Welke & Schneider 2010, 2012; but see Fromhage et al. 2003 and Foellmer & Fairbairn 2004). While many sexually cannibalistic species also exhibit extreme SSD, not all spider species exhibiting SSD perform sexual cannibalism (Wilder & Rypstra 2008). Interestingly, despite the abundance of work carried out on the evolution of SSD in spiders, very few studies have examined hypotheses relating pre- and/or post-copulatory fitness benefits with female and male size (but see Schneider et al. 2000).

Crab spiders (family Thomisidae) exhibit some of the most extreme examples of SSD among animals (Legrand & Morse 2000). Females seldom cannibalize their mates, making adaptive sexual cannibalism unlikely to account for the extreme female-biased SSD observed in crab spiders. Nothing is known about size-dependent differential survival and/or mortality in this group, leaving the potential for differential male mortality wide-open. Males of several Thomisidae species are known to be protandric, maturing earlier than females (Muniappan & Chada 1970; Dodson & Beck 1993; Morse 2013). In some species, this earlier maturation seems to favor small males given that females mate only once (e.g., Morse 2010). In other species, however, females mate multiply, which could hinder the benefits associated to an early male maturation (Dodson & Beck 1993, MC Chelini unpublished data).

In this study, we expand upon the wealth of prior work assessing SSD to test the relatively unexplored hypotheses that pre- and/or post-copulatory fitness benefits select for the combination of small male size and large female size in the crab spider *M. celer*. *Mecaphesa celer* is a flower-dwelling crab spider specialized in preying upon pollinators. Males of this species are approximately one half the total body size of females, and often weigh less than 1/10th of the average female mass. Nothing is known about the evolutionary drivers of SSD in this species.

In this study, we aim to answer two specific questions. (1) Does female and/or male size influence the probability of mating and/or remating? (2) Does female and/or male size affect clutch size and offspring survival? If body size influences the probability of mating and/or remating (question 1) and if this has influenced SSD in this species, then we predict that: (1a) small males will be more likely to obtain copulations with large females than large males and (1b) females mated to large males will be more likely to accept subsequent copulation attempts than females mated to small males. If body size influences clutch size and offspring survival and this has influenced SSD in this species, then we predict that dissortative matings according to body size – specifically between large females and small males – will result in: (2a) larger clutches and (2b) offspring that will be longer lived than the offspring of other size combinations.

Methods

Animal Collection and Maintenance

We collected spiders as juveniles (3nd–5th instar) in Oxford, MS, USA, in March 2013 and Lincoln, NE, USA, in May 2013. In the laboratory, we housed spiders in individual 4 9 4 9 6 cm acrylic cages, with *ad libitum* water, and small artificial plants for perching.

All plants were composed of a ramified plastic stem with two flowers set 3 cm apart. All spiders were in a room at 26°C and 60% relative humidity, under a 14:10 light:dark cycle. We fed all individuals twice a week with juvenile crickets (*Acheta domesticus*, 1 mm, Ghann's Cricket Farms – GA, USA) and recorded the date of all molts.

Mating Trials

We conducted all mating trials between June 3rd and July 21, 2013, from 10:00 to 17:00. Trial arenas were cylindrical 12 9 7 cm (diameter 9 height) acrylic tubes. We placed the artificial plant from each female's cage in the center of the arenas prior to a trial, fixed in a square 1 × 1 cm piece of plasticine. We placed each arena on top of a small square mirror on a 20 cm of diameter rotating platform, in order to be able to observe any behavior happening on the underside of the flowers without disturbing the focal individuals. We transferred females into the arenas along with their own artificial plant. Females were usually resting on top of the flower petals inside their cage, making their transfer easy. In cases where the females were not originally on top of their plants, we transferred them gently using a soft paint brush, allowing them to climb back onto the top flower once the plant was inside the experimental arena. We then allowed females to acclimate for 5 min before introducing males. We transferred males into the arena using a soft paint brush and placed them on the stem of the artificial flower, at least 3 cm away from the females. Based on preliminary observations we determined that the decision to mate or not was made within minutes of the first contact between male and female. As such, our trials ran for 30 min, or until copulation was over in the cases where mating did occur. We cleaned arenas and mirrors with 70% ethanol and used new pieces of plasticine for each trial, to eliminate potential chemical cues.

Female and Male Size Quantification

Once all data had been collected (see *Precopulatory benefits of large female size and small male size* and *Postcopulatory benefits of large female size and small male size*.), we sacrificed all individuals by freezing them, and later transferred them to 75% ethanol. To quantify female and male size, we photographed all adult individuals using a Spot Flex digital camera (Model 15.2 64 MP; Diagnostic Instruments, Inc. 6540 Burroughs Ave, Sterling Heights, MI) mounted on a Leica DM 4000 B Microscope. Using the software ImageJ (Rasband 1997–2012) with our photographs, we took two measures of size from each adult individual: cephalothorax width (cw) and first right femur length (fl). Female and male femurs and cephalothorax widths are normally distributed variables (Shapiro–Wilk test, female cw: $w = 0.98$, p = 0.65; male cw: $w = 0.96$, p = 0.13; female fl: $w = 0.98$, p = 0.31; male fl: $w = 0.98$, p = 0.12).

Precopulatory Benefits of Large Female Size and Small Male Size

In order to test our predictions related to the precopulatory benefits of *M. celer*'s female-biased SSD, we paired each of 60 females with three distinct males, with a two-day interval between each trial. We opted for presenting males to females in a sequential order rather than simultaneously based on preliminary observations that mutual avoidance by males and a heightened state of aggressiveness of the female would often hinder copulation attempts when males were presented to the females simultaneously. Our main response variable was occurrence of copulation, but to describe the mating behavior of this species, we also took note of copulation duration, aggressiveness of females toward males, and mate guarding of females by males. Given the small size of these animals and the fact that we did not want to manipulate individuals prior to behavioral trials, we paired females and males randomly according to size and took their measurements under the microscope only after sacrificing them (see *Female and male size quantification*, above). Females and males ages varied between 2 and 15 d post-sexual maturation (average = 5 d). All females were virgin at the time of their first trial, but due to a limitation in the number of adult males available we were constrained to use some males more than once (n = 13). Virgin and non-virgin males did not differ in size (average virgin male cw = 1.48 mm, average non-virgin male cw = 1.47 mm, Two-sample *t*-test: $t = -0.57$, df = 102.12, p = 0.56; average virgin male fl = 2.89 mm, average non-virgin male fl = 2.88 mm, *t*-test: $t = -0.34$, df = 103.04, p = 0.73).

We tested the effect of male virginity on all of our response variables using a generalized linear model (GLM), with the virginity status as the predictor variable. When male virginity had an effect on the response variable, we ran the analyses using only data from matings with virgin males. When the male virginity did not have an effect on the response variable, we used the complete dataset. To test whether *M. celer*'s female-biased SSD is related to precopulatory benefits, we built two sets of models – one for each prediction:

Mate choice

To test whether small males are more likely to obtain copulations with large females than large males, we used a generalized linear model (GLM) with a Binomial distribution and a logit link function. We used female size, male size, and the interaction between these two variables as independent variables and mating success as the binomial response variable.

Probability of remating

To test the prediction that females mated to large males will be more likely to remate, we used a similar statistical approach, replacing mating success by remating success as the binomial response variable and adding the size of the second male as a predictor variable. To avoid model overfitting due to the small number of successful rematings and our large number of parameters, we ran six separate simple binomial models instead of one full model, each corresponding to one predictor variable or one interaction. For the same purposes, we treated second and third males as equivalents. We ran these analyses using the software R (R Development Core Team 2011).

Post-Copulatory Benefits of Large Female Size and Small Male Size

To test our predictions related to post-copulatory benefits of *M. celer*'s female-biased SSD, we focused on the females that had mated with only one male in the above-mentioned mating trials, and quantified two potential benefits: (2a) clutch size, and (2b) spiderling survival. To quantify clutch and survival, we kept all females alive for up to 3 months after the trials, feeding them once a week. We monitored these females three times a week to record whether they had laid an egg sac, and whether the spiderlings had hatched from their egg sac. Once the spiderlings had hatched and dispersed from the egg sac (approximately 3 d after eclosion, Muniappan & Chada 1970), we separated them from the mothers and counted them to estimate spiderling number. Egg sacs that had not hatched after 60 d were counted as a failed clutch. We preserved the remaining non-developed eggs and the egg sac in ethanol 70%, and later counted these eggs using a stereomicroscope (see *Female and male size quantification*).

After counting all live spiderlings, we housed them individually under the same conditions as the adults, but in 1 × 3 cm glass vials with a 0.5 × 2 cm strip of plastic netting for perching, and checked them every 2 d to estimate survival. We chose to keep the spiderlings with no food in order to assess their resistance to starvation. Resistance to starvation is often correlated with the amount of yolk contained in each egg and therefore with female investment in a clutch (Fox & Czesak 2000). This proxy allowed us to test the hypothesis that females invest differently in their clutches according to their own size and their mate's size. We could not assess maternal investment through the mass of recently hatched young given that *M. celer* spiderlings weigh less than 0.1 mg, making it extremely challenging to obtain a reliable measure of mass, even when averaging the mass of an entire clutch. To test whether *M. celer*'s female-biased SSD is related to postcopulatory benefits, we ran four analyses:

2a) Clutch size

We tested the prediction that dissortative matings between small males and large females will produce larger clutches in three steps. First, to test whether large females produced more eggs than small females, particularly when mated to small males, we ran a linear model (LM), using female size, male size, and their interaction as independent variables and total number of eggs as the response variable. Then, to test the effect of female and male size on the probability of a female having a successful clutch, we ran a GLM with a Binomial distribution and a logit link function, using female size, male size, and their interaction as independent variables and clutch success as the binomial response variable. To avoid having overdispersion issues, and given that we had only one spiderling number outlier (a clutch of only four spiderlings), we treated this clutch as failed and included it in this analysis. Finally, to assess whether female and male size affect the number of spiderlings hatching from a successful clutch, we focused on matings that had produced a successful clutch and ran a linear model (LM), using female size, male size, and their interaction as independent variables and number of spiderlings as the response variable. We ran these analyses using the software R (R Development Core Team 2009).

2b) Spiderling survival

To test the prediction that large females and small males will produce longer-lived offspring, we ran a Mixed Effects Cox model with the functions *Surv*, *survfit* and *coxme*, of the R software library package *sur-*

vival (Therneau, 2015). We used each clutch as a random variable, and female femur, male femur, their addition and their interaction as predictor variables.

Results

Pre-Copulatory Benefits of Large Female Size and Small Male Size

1a) Mate choice and mating behavior

All tested females (n = 60) mated with the first male introduced to them. Only one female tried to cannibalize the male, biting his leg during copulation and forcing the male down from the typical mating position (i.e., the male on the back of the female's abdomen). That particular male autotomized his leg and ran away. All females seemingly passively allowed their paired male to mount and mate them, showing no evidence of precopulatory mate choice.

Males mounted the females shortly after first touching them, with no observable stereotyped courtship behavior, and often no more than a single contact. If the female turned aggressively toward the male prior to or upon contact, the male would retreat rapidly, then slowly re-approach the female and tap on her abdomen with his first pair of legs fully extended in front of his body. Once the male touched the female's abdomen, females would accept the males' approach. Copulation started with the male climbing on the female's abdomen, then lowering his opisthosoma and front legs along the side of her body in such a manner that one of his pedipalps could be in contact with one of her genital openings, on the ventral surface of her abdomen. After the insertion of one pedipalp was complete, the male would back up onto the dorsal side of the female's abdomen, and lower himself again against her other side. Copulation lasted 22.74 min on average (min = 5, max = 82, SD = 14.89) and ended with the male descending from the female's abdomen and distancing himself rapidly. Four males remained on the female's back for periods between 45 min and 3 h after finishing their insertions. Given that no female rejected her first mate, we did not perform any statistical analysis regarding the influence of female and male size on the probability of copulation.

1b) Probability of remating

Only nine (15%) females accepted a second copulation, four with the second male only, four with the third male only, and one with both males. Females that did not remate often reacted aggressively to the approach of the male, attacking them upon contact and sometimes biting them, either forcing males to drop legs or killing them (n = 17 attacks, 10 of which resulted in male death or leg loss). Females that did not attack males usually just moved away from them, or raised their front legs in a predatory posture without striking, and males did not pursue them.

Male virginity status did not influence the probability of remating (GLM: p = 0.89, df = 55, deviance = 0.23, 1st male virginity status: p = 0.87; 2nd male virginity status: p = 0.63). Female size, male size, and their interactions did not influence the probability of remating (GLMs cephalothorax width (cw): female cw: p = 0.93, df = 56, 1st male cw: p = 0.52, df = 56, 2nd male cw: p = 0.19, df = 56, female cw * 1st male cw: p = 0.24, df = 54, female cw * 2nd male cw: p = 0.19, df = 54, 1st male cw * 2nd male cw: p = 0.59, df = 54; GLMs femur length (fl): female fl: p = 0.56, df = 56, 1st male fl: p = 0.71, df = 56, 2nd male fl: p = 0.66, df = 56, female fl * 1st male fl: p = 0.932, df = 54, female fl * 2nd male fl: p = 0.31, df = 54, 1st male fl * 2nd male fl: p = 0.60, df = 54.

Post-Copulatory Fitness Benefits

2a) Clutch size

The total number of eggs laid by females varied from 17 to 100 ($\bar{x}$ ± SE = 56.61 ± 18.24). One single-mated female never laid eggs. Male virginity status significantly influenced the total of number of eggs laid (LM: $F = 7.14$, df = 45, p = 0.01), with non-virgin males siring larger clutches than virgin males.

Considering only the subset of virgin males (n = 34), female and male size did not affect the number of eggs laid after each mating (LM cephalothorax width: $F = 0.61$, df = 29, p = 0.61, female cw: p = 0.22, male cw: p = 0.24, female cw * male cw = 0.22; LM femur length: $F = 0.43$, df = 29, p = 0.74, female fl: p = 0.49, male fl: p = 0.53, female fl * male fl = 0.48).

Out of the 49 single-mated females, only four failed to lay a successful clutch: one female never laid eggs, two females laid egg sacs that never hatched, and one female laid an egg sac containing only four live spiderlings. All of these females were smaller than average and were mated to smaller than average males. Male virginity status had no effect on the probability of laying a successful clutch (GLM: p = 0.57, df = 48, deviance = 0.31). Female cephalothorax width, male cephalothorax width and their interaction affected positively

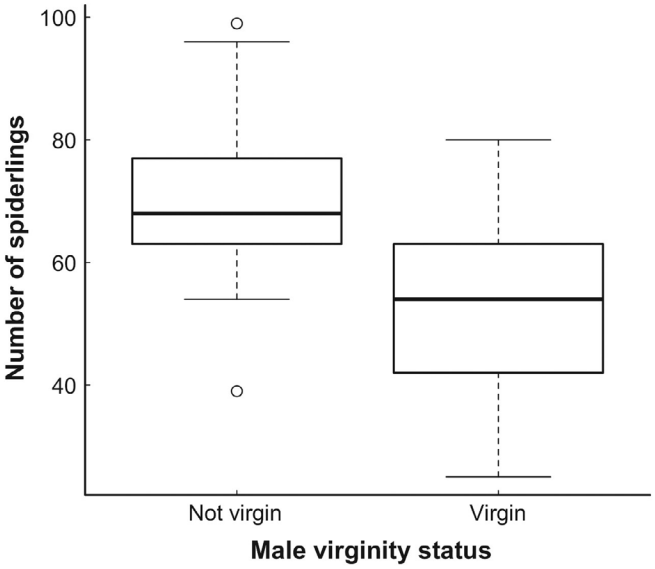

Figure 1. The relation between *Mecaphesa celer* males virginity status and the number of spiderlings sired. Boxes represent 1st and 3rd quantiles, thick black line represents the median, whiskers represent maximum and minimum without outliers.

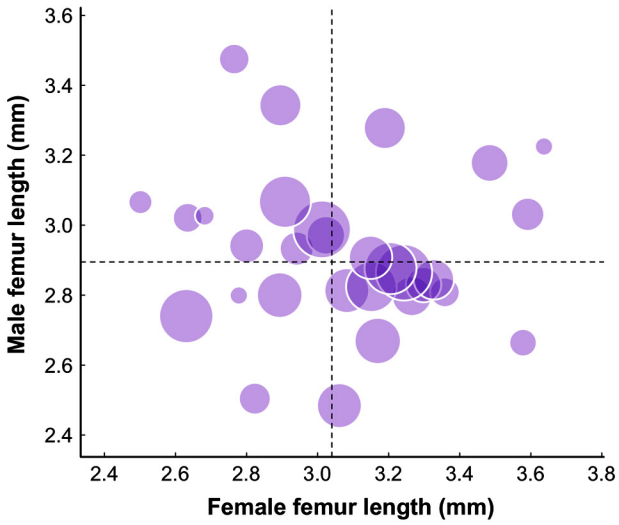

Figure 2. Number of spiderlings (represented by the diameter of the circles) in relation to female and male size. Dashed lines indicate the average size of females (vertical line) and males (horizontal lines). The bottom left and top right quadrant therefore indicate both types of assortative matings, and the bottom right and top left indicate resulting from disassortative matings.

the probability of having a successful clutch (GLM: df = 48, residual deviance = 25.07, female cw: estimate = 112.19, p = 0.02, male cw: estimate = 164.70, p = 0.02, female cw * male cw: estimate: –73.17, p = 0.02). Female femur length, male femur length, and their interaction did not affect the probability of laying a successful clutch (GLM: df = 48, residual deviance = 27.48, female fl: p = 0.11, male fl: p = 0.097, female fl * male fl = 0.12).

Spiderling number ranged from 25 to 99 ($\bar{x}$ ± SE = 58.73 ± 2.62). One female laid two egg sacs within a month (in this case spiderling number was counted as the sum of both egg sacs). Male virginity status significantly influenced the number of spiderlings (LM: F = 11.954, df = 43, p = 0.001), with non-virgin males siring more spiderlings than virgin males (Figure 1). Considering only the subset of virgin males (n = 34), female and male size did not affect the number of spiderlings resulting from each mating (Figure 2; LM cephalothorax width: F = 1.336, df = 30, p = 0.2813, female cw: p = 0.0925, male cw: p = 0.0920, female fl * male fl = 0.1012; LM femur length: F = 0.9562, df = 30, p = 0.4261, female fl: p = 0.128, male fl: p = 0.131, female fl * male fl = 0.138).

Spiderlings survival

All spiderlings died before reaching the 25th day of observation, with most losses occurring after the 9th day (average clutch survival = 15 d, min = 7, max = 23). Most clutches lost more than 50% of their spiderlings between days 9 and 13 (Figure 3). Male virginity did not affect spiderling survival (Mixed Effects Cox Model: p = 0.5858, df = 4, male virginity: p = 0.81). Male and female size did not affect spiderling survival either (Mixed Effects Cox Model cephalothorax width: p = 0.43, df = 3, female cw: p = 0.79, male cw: p = 0.88, female cw * male cw: p = 0.84; Mixed Effects Cox Model femur length: p = 0.09, df = 4, female femur: p = 0.36, male fl: p = 0.06, female fl * male fl = 0.06).

Discussion

Sexually dimorphic traits are often expected to be associated with pre- or postcopulatory fitness benefits. By testing the effect of *M. celer*'s female and male size on initial mate choice, remating behavior, clutch size, and offspring survival, we found that the SSD of this species does not appear to be driven by any of our putative pre- or postcopulatory benefits. Indeed, female size, male size, and their interaction had no effect on the probability of mating, the probability of remating, the number of spiderlings resulting from a copulation or on the survivorship of such spiderlings.

All of our initial mating trials resulted in a copulation. Not only did we not find any evidence that size is relevant for mate choice, we found that virgin female *M. celer* are apparently receptive to any male,

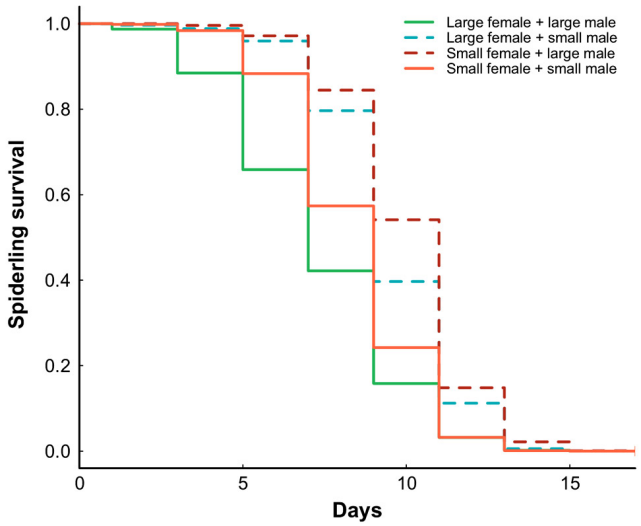

Figure 3. Survival analysis of *M. celer* spiderlings for two categories of female and male size. Solid lines represent survival of offspring from assortative matings by size; dashed lines represent survival of offspring from dissortative matings by size.

suggesting an absence of virgin female mate choice in this species. Other flower-dwelling crab spiders similarly seem to lack any type of mate choice (Dodson & Beck 1993; Morse 2007), but in at least one of these species (*Misumenoides formosipes* – Dodson & Schwaab 2001), males are known to engage in combat over the guard of subadult females. We never observed any agonistic encounter between *M. celer* males, in the laboratory or in the field, and therefore do not have any evidence that male–male competition could be the selecting mechanism leading to female-biased sexual size dimorphism in this species.

The seeming absence of virgin female mate choice in *M. celer* might be explained by their natural distribution and remating behavior. Mate choice is known to be influenced by the probability of encountering a suitable mate (Willis et al. 2011). In populations with a low female–male encounter rate, females may benefit from securing fertilization success regardless of the quality of the first male encountered (e.g., Schafer & Uhl 2004). These females may then perform sequential mate choice, becoming more selective in future encounters, mating only with males bearing preferred traits, and cryptically selecting their sperm to fertilize their eggs, or at least benefiting from the increased genetic variability of their offspring (Schneider & Elgar 1998; Jennions & Petrie 2000; Fox & Rauter 2003). The chances of encounter for male and female *M. celer* are likely to be extremely variable in the wild, given that population density can vary from less than 1 spider/20 m^2 to more than 5 spiders/1 m^2 (M.C. Chelini, unpublished data).

Only 15% of our females accepted a second mate, with 30% of the remaining mated females reacting aggressively to the males approach. Our data suggest that *M. celer* females become more aggressive and apparently choosier after an initial mating. Our observed pattern of no choice for virgin females followed by relatively few second matings might suggest, as proposed earlier, that these females are securing a first copulation and then performing cryptic female choice if a better second male is encountered. The very low percentage of female that did accept a second copulation, however, suggests that this is not a widespread strategy in *M. celer*. Moreover, we found no evidence that absolute or relative female and male size are related to remating probability, reinforcing the idea that mate choice, even in second matings, is not the selecting mechanisms leading to *M. celer*'s female-biased SSD.

Mate choice may be a costly mechanism, evolving only in systems where the benefits associated with selective mating exceed its costs (Kokko et al. 2002; Kotiaho & Puurtinen 2007). In species with relatively low encounter rates, such as *M. celer*, the simple risk of not finding a mate represents a high cost for mate choice. In the absence of pre- or post-copulatory benefits, and with mate choice being costly, we might predict an absence of mate choice. The lack of mate choice of *M. celer* is therefore quite parsimonious, given that we found no evidence that large female size and small male size are associated with higher post-copulatory benefits.

Female and male sizes were not related to the number of eggs laid, to the number of spiderlings, or to the survival of spiderlings. The probability of success of a clutch, however, was affected to the body size of males and females, as well as by their interaction, but not by leg length. Morse (2013) found that small *Misumena vatia* (Thomisidae) females often failed to lay clutches in the field even when mated, probably because their poor condition hindered their fecundity. When supplied with food, these females readily laid fertilized clutches. It is possible that very small *M. celer* are unable to produce clutches; however, size had no effect on the total number of eggs laid, indicating that failing to lay a successful clutch is not related to small females being unable to produce, or lay eggs, but on the interaction between female egg production and male fertilization success. Small males have been shown to fertilize more eggs in other extreme sexually dimorphic spider species (e.g., Elgar et al. 2000; Schneider et al. 2000), but our results suggest that any relationship between male size and fertilization success is likely species specific. Although this result points to an interesting in-

teraction between female and male effects, we would like to acknowledge that our very low number of failed clutches (n = 4) and the relatively high number of parameters in our model ($k = 3$) may be resulting in model overfitting and Type II error. Nonetheless, these are interesting results that should be further explored in future studies with larger sample sizes.

Surprisingly, however, we found a positive relationship between male mating status and clutch size, with non-virgin males having larger clutches than virgin males. Assuming that this is a male-driven pattern, we can only speculate that given the potentially high costs of mate search, and the spatially uneven distribution of females in the wild, virgin males could be retaining sperm in their first copulation in order to be able to remate if a second female is found in a short period of time. Indeed, male crab spiders typically require a period of a few hours to a day to recharge their pedipalps with sperm before being able to remate (Morse 2007). Interestingly, the total number of eggs laid was also affected by male virginity status, suggesting that this pattern may be at least partially female-driven. It is possible that females lay more eggs when mated to a non-virgin, more successful male. Future work is required to test these hypotheses.

The lack of relationship between female size and number of spiderlings is our most surprising result. The fecundity hypothesis for large female size (Head 1995) posits that large females should always have more offspring than small females (e.g., Beck & Connor 1992; Skow & Jakob 2003), a pattern so common that is has been considered the main driver of female-biased SSD in spiders (Prenter et al. 1999). In his classic paper challenging the fecundity advantage model, Shine (1988) proposed that the fecundity advantage model may hold only in scenarios where females are not limited energetically, and points out that a larger number of eggs in one clutch is not the same as a higher lifetime reproductive success. Although *M. celer* has only one reproductive season, females may lay up to four egg sacs following a single copulation (M.C. Chelini, unpublished data). The fact that only one female laid a second egg sac in our experiment could suggest that our feeding regimen was too strict for these females to achieve their maximum reproductive potential; a possibility that should be followed up on in future studies.

Other exceptions to the fecundity advantage model occur when females trade quantity for quality in their clutches, investing more in each egg instead of increasing egg numbers. If large *M. celer* females were trading egg quantity with egg quality, we would expect to find an effect of female size on spiderling survival. Our results, however, show that female size, male size, and their interaction have no effect on spiderling survival, contradicting the last of our predictions. One possibility is that spiderling survival to starvation is not a good proxy of post-copulatory fitness benefits in *M. celer*. Alternatively, female and male size may indeed not be the determinants of spiderling survival. Offspring survival has been related to factors as disparate as female age (e.g., fishes: Berkeley et al. 2004; lizards: Olsson & Madsen 2001), past maternal condition (butterflies: Bonduriansky & Head 2007), and polyandry (crickets: Ivy & Sakaluk 2005). As such, female and male *M. celer* may still have an effect on offspring survival, even if their influence is not relative to their size.

Altogether, our results suggest that *M. celer*'s large female size and small male size must have been selected by factors other than mate choice and postcopulatory benefits. In a species where virgin females mate indiscriminately and polyandry is relatively rare, a shortened development time is likely to benefit small males (Blanckenhorn 2000). As such, adaptive protandry is likely to be the mechanism selecting for *M. celer*'s female-biased sexual size dimorphism. In-depth studies on the synchrony of development of this species in the wild, as well as on the potential for sperm competition in polyandrous females, are currently underway and should shed light into the evolution of this intriguing study system.

In summary, dimorphic traits are often assumed to be associated to reproductive benefits. Examples of dimorphic traits providing direct benefits are abundant, as are models associating traits that do not confer direct benefits to indirect benefits (see Jones & Ratterman 2009 and references therein). Here we present a study species that contradicts several predictions drawn from the evolutionary theory of sexual size dimorphism. In highly conserved clades, and in the absence of clear costs or benefits associated with a dimorphic trait, species may be dimorphic simply by effect of non-directional evolution (Brownian motion evolutionary model: Felsenstein 1973), as has been recently described by Cheng & Kuntner (2014) with regard to the sexual size dimorphism of the Argiopinae family of orb-weaving spiders. As such, given that SSD is common in the clade of flower-dwelling crab spiders, *M. celer*'s extreme SSD may not be associated with any current pre- or post-copulatory benefit and may simply be a consequence of relaxed selection on an ancestral character. Unfortunately, given that SSD is yet to be mapped on a family-, or even genus-wide phylogeny, we can currently only speculate on the direction and strength of selection acting upon *M. celer*'s SSD.

We can also use *M. celer* as a precautionary tale against our inner bias toward studying species where the most eye-catching trait is associated to evident benefits. Our understanding of SSD evolution, and of any dimorphic trait, depends on the study and publication not only of eye-catching exceptions (see Huber 2005), but also of theory-defying cases such as this present study.

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